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Nutrient Studies in Relation to Habitat Types and Canopy Dieback in the Montane Rain Forest Ecosystem, Island of Hawai'i[1]

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ABSTRACT: A soil and foliar nutrient analysis was carried out in the Hawaiian *Metrosideros* rain forest for the purposes of elucidating a previously published physical habitat classification and for finding an explanation for the widespread canopy dieback, which is not caused by a biotic agent in this ecosystem. Soil elements analyzed were C, N, P, Ca, Al, Mn, Fe, and other parameters such as pH. Foliar analysis was restricted to N, P, Ca, Mn, and Fe and assessed only for the canopy *M. polymorpha* and its major associate, the tree ferns, in the undergrowth. It was found that the earlier recognized two-way breakdown into oligotrophic and eutrophic nutrient regimes had to be enlarged for the habitat classification to a mesotrophic category. Young, deep-ash soils were recognized as mesotrophic on account of their moderate pH and high Ca levels, but they showed severe limitations in available nitrogen and phosphorus that were reflected also in the foliage. Intermediate-aged (1000 yr) ash soils were found to be nutritionally well supplied and balanced and thus considered eutrophic, while older ash soils were designated as oligotrophic on account of their extreme acidity and associated higher and potentially toxic levels of soluble Al, Mn, and Fe. Except for the mesotrophic 'a'ā lava site, other shallow rock outcrop habitats on pāhoehoe were recognized as oligotrophic, because of very low available N and high acidity and, in the poorly drained sites, also high levels of potentially toxic metals. The bog habitats had the highest levels of potentially toxic metals, but surprisingly moderate levels of available N and P. The canopy dieback phenomenon cannot be entirely explained from the nutrient imbalances found in most of the substrate types, but these imbalances are considered contributory in the sense that they become increasingly stressful with stand development, thereby decreasing tree vigor and predisposing stands to dieback.

THE WIDESPREAD CANOPY DIEBACK in the Hawaiian *Metrosideros* rain forest was initially considered a biotic disease problem (Petteys, Burgan, and Nelson 1975). However, after intensive research, biotic agents were thought to be of lesser importance (Hwang 1977, Papp et al. 1979), and attention was drawn to soil nutrients. Kliejunas and Ko (1974) found that dying trees could be revived with NPK fertilizer, but not with application of fungicide. Earlier in this century, a *Metrosideros* canopy dieback on the island of Maui was also recognized as a nutrient problem rather than a biotic disease problem. Lyon (1909, 1918), a researcher for the Hawaiian Sugar Planters Association, spent several years investigating the Maui dieback. He concluded that native tree stands were dying because of soil toxicity developing with soil aging and poor drainage.

Ecological studies carried out on the islands of Hawaii and Maui established that the soils in the dieback territories vary con-

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siderably from well-drained lava rock outcrop to boggy soils. As a framework for further studies, a habitat classification was derived (Mueller-Dombois 1981, Mueller-Dombois et al. 1980), which is briefly explained in the section titled "Study Area and Habitat Types." In conjunction with this habitat classification, five kinds of canopy dieback were recognized. These were called "dryland" dieback, "wetland" dieback, "displacement" dieback, "bog-formation" dieback, and "gap-formation" dieback (Mueller-Dombois 1981; Mueller-Dombois, this issue).

Mueller-Dombois (1982) has proposed the "cohort senescence" theory for explaining canopy dieback as a naturally recurring mechanism in the succession processes of the Hawaiian *Metrosideros* rain forest. According to this theory, cohort senescence implies a uniform loss of vigor of a canopy cohort due to a combination of aging and gradually increasing environmental stress. When cohort stands are predisposed to die because of their senescence, additional factors may precipitate or aggravate canopy dieback. The latter are considered to be fluctuating site factors ("triggers") such as a local storm, root flooding, or a temporary soil drought that may kill a senescing but not a vigorously growing stand. In this theory, nutritional limitations are considered an important predisposing stress in stand development. Therefore, nutrient studies were suggested as being of particular importance.

The objectives of this study were twofold. The first objective was to establish a nutrient data base associated with the habitat types. The second objective was to find out whether soil chemistry can be considered a stress factor in predisposing stands to dieback.

Field research led to two sets of hypotheses that further guided this nutrient study:

(1) In the habitat classification, nutrient regimes for soils derived from volcanic ash were divided into oligotrophic and eutrophic from observations of soil profiles, pH measurements, and growth responses in the vegetation. We hypothesized that this nutrient regime classification would be supported by the new data presented in this paper.

(2) Among the canopy dieback types, we considered the dryland and gap-formation diebacks to be affected by limitations in soil nutrients—in particular, by low nitrogen and low phosphorus availability. This hypothesis was based on the experimental results of Kliejunas and Ko (1974), who reported inorganic nutrients to be a factor in *Metrosideros* dieback. In their case, dieback was studied in a low-stature pioneer stand growing on a young pāhoehoe flow that originated in 1855. At the other end of the habitat spectrum, we considered wetland dieback and bog-formation dieback to be affected by soil toxicity, particularly by reducing iron. This hypothesis was based on the observations of Lyon (1909). Finally, we hypothesized that displacement dieback, which occurs on what we recognized as eutrophic fine-textured ash, is not affected by any nutrient limitations or toxicities.

STUDY AREA AND HABITAT TYPES

The nutrient study was done in the general dieback terrain of the montane rain forest on the windward side of the island of Hawaii, which has been described in several previous publications (Mueller-Dombois et al. 1980, Petteys et al. 1975). It is the same forest area (of about 100,000 ha) portrayed on the map (Figure 1) in Jacobi, Gerrish, and Mueller-Dombois (this issue). This map shows three generalized habitats associated with three of the dieback types (wetland, bog-formation, and displacement). Sample plots outside these three generalized habitats and dieback types fall into either the dryland (= well drained) or gap-formation areas, which were not separated on the map. The latter often occur on knolls and ridges in the boggy terrain on Mauna Kea.

The entire area was previously classified into a number of hierarchically arranged habitat types (Mueller-Dombois 1981, Mueller-Dombois et al. 1980). An overview is given in Table 1. The habitat types are separated into two major categories, those on shallow soils and those on deep soils. This separation is based on a mean soil depth of

TABLE 1

HABITAT CLASSIFICATION AND KINDS OF 'ŌHI'A FOREST DIEBACK: AN OVERVIEW
(from Mueller-Dombois 1981)

IMPORTANT HABITAT VARIATIONS			RELEVÉS	DIEBACK TYPE
Shallow-soil habitats with lava rock outcrop	Pāhoehoe lava	Type I Poorly drained	1, 3, 11, 15, 25, 27, 28, 34, 35, 36, 37, 53	Wetland
		Type II Well drained	12, 13, 14, 16 50, 51, 54	Dryland
		Type III Poorly drained	6, 7, 10, 24, 39, 43, 52	Wetland
	'A'ā lava	Type IV Well drained	23, 33, 55	Dryland
		Type V Coarse-textured	18, 20, 26, 30	Dryland
Deep-soil habitats without lava rock outcrop	Eutrophic ash	Type VI Fine-textured	21, 22, 29, 31, 32, 38, 44, 56	Displacement
		Type VII Knoll and ridge habitats	4, 5, 8, 41, 42, 45, 60, 61	Gap-formation
	Oligotrophic ash	Type VIII Low-lying ridges and slopes	19, 47, 49	
	Bog	Type IX Clay soil bogs	17, 46	Bog-formation
		Type X Organic soil bogs	2, 40, 48, 59, 62	

NOTE: Not included are habitats on very recent volcanic substrates, i.e., those with dates recorded since 1790 (known locally as "historic" lava flows or ash beds).

50 cm over bed rock. The shallow-soil habitats are further separated into pāhoehoe and 'a'ā lava types. These are chemically similar volcanic rock types (basalts), but they differ physically. The pāhoehoe is a smooth, pavementlike lava broken into polygonal blocks. Initially, this lava is well drained, but when the fissures become sealed with fine ash particles and organic matter, they may become poorly drained. These drainage differences are recognized in the classification (see types I and II in Table 1). 'A'ā is a clinkerlike substrate with properties that readily permit water percolation at the surface. But when spaces between clinkers are clogged with ash and organic matter, they also may become poorly drained, resulting in a habitat difference recognized in types III and IV (Table 1).

The deep-soil habitats are all from volcanic ash deeper than 50 cm. They were separated into eutrophic (nutritionally rich) and oligotrophic (nutritionally poor) on account of their differences in incorporated organic matter and levels of soil acidity. A third type of

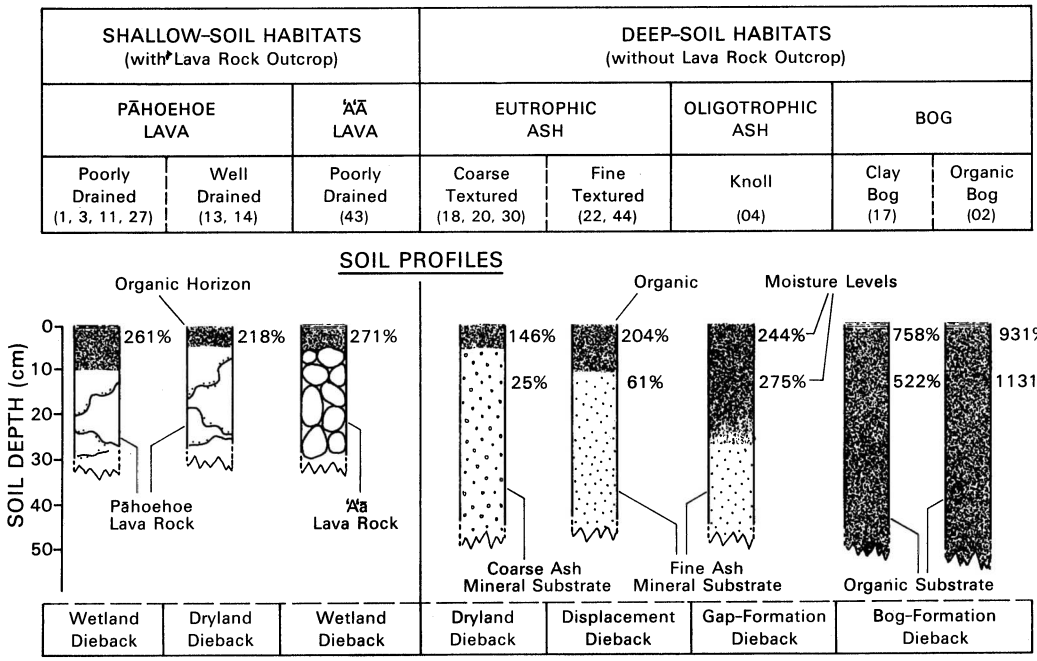

FIGURE 1. Habitat classification with idealized soil profile sketches for eight of the ten habitat types selected for this nutrient study. Coarse ash refers to loamy sand texture with inclusions of fine gravelly ash. Fine ash refers to clay-textured material. Other terms explained in text.

deep-ash substrate was permanently water soaked and distinguished as bog habitat. Finer breakdowns within these three groups are based on texture, land form, and amount of unincorporated organic matter. Overall, this resulted in ten easily recognizable habitat types (identified as types I–X in Table 1).

Figure 1 gives a further characterization of eight of the ten habitat types, which were sampled for the nutrient study. Notice the same hierarchical breakdown starting with shallow-soil and deep-soil habitats. Soil profiles are typified for each habitat type by depth of unincorporated organic matter, parent material, texture, and soil moisture. Habitat and dieback type relationships are indicated at the bottom, and the sample plot numbers are recorded above the profiles.

MATERIALS AND METHODS

Of the 62 relevés (sample stands) listed and classified by habitat type in Table 1, 15 were selected for the nutrient study. The selected relevés represent 8 of the 10 habitat types. This subsample gives a fair representation of the site spectrum in the dieback terrain.

Soil samples were taken at 20 randomly chosen points along two 20-m transects within each relevé. At each point, a sample of the unincorporated organic layer was taken with a 6-cm-diameter soil corer. In the shallow-soil habitats, the corer was pushed down to the underlying lava surface; in the deep-soil habitats, the corer was pushed to the surface of the underlying mineral soil. Separate cores of the mineral soil beneath the organic layer were also taken in the deep-ash soils at the same sampling points. For the bog soils, however, cores were collected from the soil surface to depths of 0–10 cm and 10–20 cm. Horizon depth was also determined at each sampling point.

Subsequently, each sample was divided in half, and one portion was used for determining moisture content, while the other was used for chemical analyses. From the dry

weight and volume relations of each sample, bulk density was calculated, and this together with the depth measures served to establish the horizon mass for each relevé. The other sample portion was further treated by randomly combining four samples for each horizon per relevé. These composite samples were used for chemical analyses.

Laboratory Soil Analyses

For all composite samples, soil pH was measured in water 1 : 1 using glass electrodes. This work was done in Hawaii, but the remaining analyses were done in the Forest Soils Laboratory, University of Alaska, Fairbanks. Soil organic carbon was determined in a Leco induction furnace from air-dried samples ground in a ball mill. For total N and P, subsamples were digested in a selenious acid–sulfuric acid–water mixture using a Technicon block digestor. The digestates were determined colorimetrically by use of the Technicon autoanalyzer. Calcium was estimated on the digestates by atomic absorption spectrometry following procedures outlined in Price (1978). This was done similarly for K and Mg, but the latter elements will be reported elsewhere. Exchangeable Ca, Mn, and Fe were determined by displacing the cations with 1N NH_4OAc (pH 7). The displaced cations were measured by atomic absorption spectrophotometry. Potassium chloride (2N) extracted Al and water-extracted Mn and Fe (Black 1965) were also determined by atomic absorption spectrophotometry. Both the ammonium acetate and the water extraction methods were used to estimate Fe in its ferrous form, which is soluble. The fixed or unsoluble form of Fe, referred to as ferric iron, was not measured. Available P was analyzed by NH_4F extraction and determined colorimetrically by use of the Technicon autoanalyzer.

Soil Incubations for Other Nitrogen Parameters

Five-gram soil samples were placed in 100 ml 2N KCl for 24 hr. The extracts were centrifuged to get the clear supernatant for chemical analyses. Three replicates were prepared for each composite sample. Another set of subsamples (5 g) were placed in polyethylene cups closed with a lid containing a pinhole. These were incubated at 17°C for a period of 30 days in the dark. The moisture levels of the samples were maintained at the field level gravimetrically. At the end of the incubation period, samples were extracted in KCl as described above. These procedures for determining nitrogen mineralization potentials were adapted from Vitousek et al. (1983). One drop of toluene was added as preservative to each vial containing the supernatant KCl extract. The vials were then shipped to Fairbanks for chemical analyses.

The NH_4–N and NO_3–N levels were determined colorimetrically on each sample using the Technicon autoanalyzer. After incubation for 30 days, net nitrogen mineralized was calculated as the final NH_4–N plus NO_3–N minus the initial NH_4–N plus NO_3–N (Vitousek et al. 1983). Nitrification was calculated as the final NO_3–N minus the initial NO_3–N.

Foliar Sampling

Mature, undamaged, healthy leaves were taken from tall healthy *Metrosideros* canopy trees. Shade leaves were avoided. Two to five trees were sampled, depending on the number of available healthy trees in each study site. From each tree, several branches were selected and several independent composite samples of leaves were made for each relevé. Tree fern fronds were also sampled.

In the laboratory, the leaves and frond pieces were rinsed quickly with deionized water and dried at 70°C using a forced draft oven. The dried tissues were ground using a Wiley mill and stored in bottles for chemical analyses.

Foliar Chemical Analyses

Analyses were done in the Department of Botany, Hawaii Institute of Tropical Agriculture and Human Resources. The ground samples were used for determining Ca, Fe, and Mn by weighing a subsample and ashing

it overnight in a muffle furnace at 475°C. The ashed samples were dissolved in 4N HCl, filtered, and made to volume. On aliquots of this solution, the concentrations of Ca, Mn, and Fe were determined with an atomic absorption spectrometer.

For P and N, 0.25-g samples were digested in the Block digestor (Schuman, Stanley, and Knudsen 1973) using 7 ml of digestion mixture, 5 drops of sodium thiosulfate solution, and 4 ml of H_2O_2. The 7 ml digestion mixture consisted of 5 g SeO_2 and 65 g salicylic acid added to a full bottle (approx. 2.2 liters) of reagent H_2SO_4. This mixture was prepared by briefly shaking it and then letting it stand for 1 week. After digestion, volume was made to 25 ml, left standing overnight, and then P and N concentrations were determined using the Technicon autoanalyzer.

RESULTS

The results are summarized in Tables 2–6. Eight (of the ten) habitat types sampled for this study are listed in the first column of each table. The corresponding relevé numbers are listed in the second column. The third column identifies the nature of the soil horizon as either organic or mineral, and the fourth column gives the horizon depth for each sample (except in Table 5). The remaining columns give mean values of the nutrient factors and related parameters analyzed for this study.

Table 2 presents three soil parameters: bulk density, pH, and soil moisture. It also includes five habitat descriptors: mean annual rainfall, air temperature, elevation of each relevé, its approximate substrate age, and current vegetation structure. The habitat types were differentiated to some extent by depth of unincorporated organic surface layers. The shallowest surface layers (5–6 cm deep) were found on the well-drained pāhoehoe sites (type II, relevés 13 and 14), while on poorly drained pāhoehoe (type I), depths tended to be deeper (8–16 cm). As expected, the bog habitat types showed the deepest organic layers. Even in what we have identified as clay bog (habitat type IX, relevé 17), the organic layer exceeded that of the deepest measured on poorly drained pāhoehoe. The organic layers in the remaining habitat types (III, V, VI, and VII) generally were intermediate in depths between the well-drained and poorly drained pāhoehoe (ranging from about 7 to 12 cm).

The bulk density values do not reflect any habitat differences other than those correlated with the nature of the organic layer. Most organic layers show bulk density values less than 0.4 g/cm^3. Higher values for organic layers are found on some ash soils, here indicating greater mixing with mineral soil.

The pH values again exhibit trends related to habitat type. The most acid reactions (<pH 4) were recorded in the oligotrophic ash habitat (type VII). The bog habitats compared well in acidity with the shallow-soil habitat types (I, II, and III), which ranged from pH 4.0 to 5.1. Higher soil pH values (5.2–6.0) were characteristic for the eutrophic ash habitat types (V and VI).

Not too much weight can be given to the soil moisture values since they represent one-time means. However, they give an indication of the enormous quantity of water that can be held in the unincorporated organic matter of these habitat types; for example, 932% in the organic bog (type X), or 774% in the organic layer on poorly drained pāhoehoe (type I, relevé 1). On well-drained pāhoehoe, the moisture content was considerably less, but still high, with values exceeding 200%.

The five habitat descriptors (rainfall, temperature, elevation, substrate age, and vegetation structure) elucidate additional variations within and between habitat types, which can in part be interpreted as environmental gradients. For example, the deep-soil habitat types (V, VI, VII, IX, and X) portray a three-step soil-age sequence, which coincides with their separation into three habitat groups: eutrophic coarse-textured (191 yr), eutrophic fine-textured (1000 yr), and oligotrophic ash and bogs (>4000 yr). Geographically, these habitat types extend from south to north in the study area, all in the same temperature regime, but coinciding with a rainfall gradient from 2000 to 5100 mm. A similar relationship exists among the shallow-soil habitats. The

TABLE 2

SUMMARY OF SELECTED HABITAT PROPERTIES

HABITAT TYPES (DIEBACK TYPES)	RELEVÉ	HORIZON	HORIZON DEPTH (cm)	BULK DENSITY* (g/cm³)	pH†	MOISTURE† (%)	RAINFALL (mm)	AIR TEMPERATURE‡ (°C)	ELEVATION [m (ft)]	SUBSTRATE AGE§ (yr)	VEGETATION
I. Pāhoehoe—poorly drained (wetland dieback)	1	Org	0–10	0.13	4.5	774	5,100	16–17	1,160 (3,800)	3,500	Open canopy, moderate stature; matted ferns
	3	Org	0–8	0.14	4.0	495	5,100	16–17	1,160 (3,800)	>3,500	Open canopy, moderate stature; matted ferns
		Org	8–16	0.22	4.1	345					
	11	Org	0–8	0.26	4.8	323	4,300	17–18	1,040 (3,400)	>1,500?	Very open canopy, tall stature; high % matted fern
	27	Org	0–9	0.34	5.1	261	4,300	18–19	915 (3,000)	1,500	Closed canopy, tall stature; high % tree fern
II. Pāhoehoe—well drained (dryland dieback)	13	Org	0–5	0.24	4.5	218	3,800	14–15	1,525 (5,000)	500?	Closed canopy, tall stature; low % tree fern
	14	Org	0–6	0.23	4.3	233	3,800	14–15	1,525 (5,000)	>500?	Closed canopy, tall stature; low % tree fern
III. ʻAʻā—poorly drained (dryland dieback)	43	Org	0–7	0.30	5.1	271	4,300	17–18	990 (3,250)	>1,500?	Closed canopy, tall stature; high % tree fern
V. Eutrophic ash—coarse-textured (wetland dieback)	18	Org	0–7	0.36	5.5	146	2,000	16–17	1,190 (3,900)	191	Open canopy tall stature; high % tree fern
		Min	7–12	1.35	5.9	25					
	20	Org	0–6	0.55	5.6	103	2,000	16–17	1,190 (3,900)	191	Closed canopy, tall stature; high % tree fern
		Min	6–12	1.49	6.0	16					
	30	Org	0–10	0.44	5.6	137	2,000	16–17	1,190 (3,900)	191	Closed canopy, tall stature; high % tree fern
		Min	10–15	1.33	5.9	21					
VI. Eutrophic ash—fine-textured (displacement dieback)	22	Org	0–10	0.40	5.2	204	3,000	16–17	1,220 (4,000)	1,000	Closed canopy, tall stature; high % tree fern
		Min	10–13	1.14	5.7	62					
	44	Org	0–12	0.36	5.2	230	3,000	16–17	1,220 (4,000)	1,000	Open canopy, tall stature; high % tree fern
		Min	12–16	1.16	5.7	65					
VII. Oligotrophic ash—(gap-formation dieback)	4	Org	0–7	0.20	3.5	244	5,100	16–17	1,160 (3,800)	>4,000	Closed canopy, tall stature; low % tree fern
		Org	7–12	0.29	3.7	275					
IX. Clay bogs—(bog-formation dieback)	17	Org	0–10	0.14	4.8	758	5,100	16–17	1,190 (3,900)	>4,000	Open, low-stature trees
		Org	10–20	0.19	4.8	523					
X. Organic soil bogs—(bog-formation dieback)	2	Org	0–10	0.13	5.1	932	5,100	16–17	1,160 (3,800)	>4,000	Open treeless bog

NOTE: Habitat types IV and VIII are not included. Org = organically enriched surface soil layer; Min = mineral soil below-surface soil layer.

*Mean values of 20 measurements.

†Mean values of 5 samples of one-time measurements.

‡Calculated from lapse rate.

§Best approximation (from Geological Surveys, Volcanoes Observatory, Hawaii).

TABLE 3

SOIL NITROGEN POOL SIZES AND CONCENTRATIONS AND FOLIAR NITROGEN CONCENTRATIONS FOR DIFFERENT HABITAT TYPES

HABITAT TYPES (DIEBACK TYPES)	RELEVÉ	HORIZON	HORIZON DEPTH (cm)	HORIZON MASS (kg/m^2)	ORG C AMT. (kg/ha)	ORG C CONC. (%)	TOTAL N AMT. (kg/ha)	TOTAL N CONC. (%)	C:N	NH_4–N AMT. (kg/ha)	NH_4–N CONC. (%)	NO_3–N + NO_2–N AMT. (kg/ha)	NO_3–N + NO_2–N CONC. (%)	FOLIAR N: CANOPY TREE CONC. (ppm)	FOLIAR N: UNDERSTORY TREE FERN CONC. (ppm)
I. Pāhoehoe—poorly drained (wetland dieback)	1	Org	0–10	12.4	42,474	34	2,369	1.90	17.6	2.79	24	0.0	0.0	n.d.	n.d.
	3	Org	0–8	11.4	45,864	40	2,002	1.74	22.9	0.80	6	1.08	11.2	9,600	15,400
		Org	8–16	17.9	42,939	24	2,521	1.41	17.1	0.98	8	1.43	8.7		
	11	Org	0–8	20.7	40,017	20	2,039	1.03	20.0	1.60	8	0.0	0.0	7,100	13,200
	27	Org	0–9	30.5	45,498	15	2,839	0.95	17.5	4.23	13	0.84	2.6	8,700	13,700
II. Pāhoehoe—well drained (dryland dieback)	13	Org	0–5	9.9	34,134	35	1,248	1.27	27.5	2.45	24	0.0	0.0	6,400	11,500
	14	Org	0–6	13.9	57,119	41	1,928	1.39	29.9	1.54	11	0.0	0.0	7,000	16,800
III. ʻAʻā—poorly drained (wetland dieback)	43	Org	0–7	19.7	41,004	22	2,320	1.18	19.4	1.85	10	1.96	10.2	10,600	15,400
V. Eutrophic ash—coarse-textured (dryland dieback)	18	Org	0–7	25.0	27,387	11	1,446	0.58	19.3	2.46	10	0.02	0.1	6,800	13,600
		Min	7–12	67.7	6,672	1	746	0.11	8.9	1.33	2	0.0	0.0		
	20	Org	0–6	26.0	32,691	13	1,805	0.64	15.6	1.24	5	0.07	0.3	6,500	13,500
		Min	6–12	80.5	13,185	2	1,623	0.19	9.7	0.58	1	0.0	0.0		
	30	Org	0–10	43.9	39,607	9	2,890	0.66	13.5	7.83	19	0.45	1.1	7,500	15,300
		Min	10–15	68.6	17,527	3	1,182	0.17	15.0	1.49	1	0.37	0.5		
VI. Eutrophic ash—fine-textured (displacement dieback)	22	Org	0–10	40.4	49,589	12	3,816	0.96	13.0	2.00	5	7.03	17.7	12,800	18,900
		Min	10–13	39.5	10,457	3	960	0.24	10.9	0.21	1	0.89	2.1		
	44	Org	0–12	43.8	52,863	13	4,601	1.12	11.6	2.46	6	6.43	15.6	11,400	15,500
		Min	12–16	44.8	13,308	3	1,208	0.27	11.3	0.61	1	1.02	2.4		
VII. Oligotrophic ash—(gap-formation dieback)	4	Org	0–7	14.2	55,229	40	2,383	1.69	23.1	2.68	19	1.28	8.3	9,300	15,700
		Org	7–12	13.8	20,327	15	1,311	0.96	15.5	0.82	6	1.68	12.3		
IX. Clay bogs—(bog-formation dieback)	17	Org	0–10	12.5	45,919	37	2,433	1.96	18.8	0.89	8	0.00	0.0	7,800	n.d.
		Org	10–20	18.6	47,097	25	2,463	1.32	19.0	0.48	3	0.00	0.0		
X. Organic soil bogs—(bog-formation dieback)	2	Org	0–10	12.9	39,617	32	2,763	2.15	14.7	4.17	36	0.19	1.2	n.d.	n.d.
		Org	10–20	13.8	46,745	35	3,020	2.25	15.5	10.05	72	0.31	0.2		

NOTE: Habitat types IV and VIII are not included. The values are means of 5 independent composite samples for soils and means of 5–10 independent composite samples from mature leaves on healthy trees for foliar concentrations; n.d. = not determined; ppm = % multiplied by 10,000.

TABLE 4

NET MINERALIZATION POTENTIALS AND NITRATE PRODUCTION FOR INCUBATED SOILS FROM DIFFERENT HABITAT TYPES

HABITAT TYPES (DIEBACK TYPES)	RELEVÉ	HORIZON	HORIZON DEPTH (cm)	NET MINERAL N PRODUCTION		NITRATE N PRODUCTION	
				AMT. (kg/ha)	CONC. (ppm)	AMT. (kg/ha)	CONC. (ppm)
I. Pāhoehoe—poorly drained (wetland dieback)	1	Org	0–10	−0.19(1.25)	−3.90(7.90)	2.05(0.83)	15.30(5.00)
	3	Org	0–8	−0.70(1.11)	−8.80(7.80)	−1.05(1.08)	−10.90(1.60)
		Org	8–16	0.62(0.38)	3.60(2.20)	−0.12(0.55)	−0.90(0.30)
	11	Org	0–8	−0.27(0.44)	−1.50(2.10)	0.00(0.00)	0.00(0.00)
	27	Org	0–9	−1.25(0.49)	−4.00(1.60)	1.42(1.20)	4.00(3.10)
II. Pāhoehoe—well drained (dryland dieback)	13	Org	0–5	−1.40(1.12)	−14.10(11.40)	0.00(0.00)	0.00(0.00)
	14	Org	0–6	0.03(0.07)	0.25(0.47)	0.00(0.00)	0.00(0.00)
III. ʻAʻā—poorly drained (dryland dieback)	43	Org	0–7	2.46(0.47)	10.10(4.60)	3.12(2.20)	13.70(3.50)
V. Eutrophic ash—coarse-textured (wetland dieback)	18	Org	0–7	−1.13(0.30)	−4.80(1.30)	0.05(0.04)	0.25(0.24)
		Min	7–12	−1.17(0.62)	−1.60(0.80)	0.03(0.03)	0.05(0.05)
	20	Org	0–6	−0.02(0.06)	−0.10(0.20)	−0.07(0.04)	−0.26(0.15)
		Min	6–12	2.18(1.86)	2.70(2.40)	0.00(0.00)	0.00(0.00)
	30	Org	0–10	−5.91(0.94)	−14.30(3.30)	0.39(0.40)	0.69(0.83)
		Min	10–15	−1.42(0.32)	−2.00(0.30)	−0.30(0.25)	−0.39(0.31)
VI. Eutrophic ash—fine-textured (displacement dieback)	22	Org	0–10	4.15(1.62)	9.60(3.40)	4.57(1.63)	10.70(3.40)
		Min	10–13	1.20(0.90)	1.50(0.90)	0.44(0.66)	1.10(0.10)
	44	Org	0–12	4.70(0.59)	11.60(1.60)	5.67(0.70)	14.00(1.90)
		Min	12–16	1.46(1.65)	3.90(3.60)	1.03(0.53)	2.50(1.50)
VII. Oligotrophic ash—(gap-formation dieback)	4	Org	0–7	9.73(2.40)	68.50(15.00)	1.93(1.11)	14.40(8.50)
		Org	7–12	2.89(0.59)	21.80(5.80)	2.46(0.43)	18.20(3.70)
IX. Clay bogs—(bog-formation dieback)	17	Org	0–10	0.55(0.70)	5.30(6.30)	0.82(0.28)	7.50(2.50)
		Org	10–20	0.23(0.15)	1.30(0.90)	0.16(0.10)	0.80(0.20)
X. Organic soil bogs—(bog-formation dieback)	2	Org	0–10	1.28(0.54)	10.10(3.10)	4.23(0.01)	41.90(7.00)
		Org	10–20	−0.78(0.26)	−5.90(6.80)	7.31(2.00)	52.20(12.70)

NOTE: Habitat types IV and VIII are not included. The values reported are means (± standard errors) of 5 independent composite soil samples; ppm = % multiplied by 10,000; ppm = μg/g.

TABLE 5

POOL SIZES AND CONCENTRATIONS OF SOIL ALUMINUM, CALCIUM, AND PHOSPHORUS, AND FOLIAR CONCENTRATIONS OF CALCIUM AND PHOSPHORUS FOR DIFFERENT HABITAT TYPES

HABITAT TYPES (DIEBACK TYPES)	RELEVÉ	HORIZON	pH	SOIL Al, KCl EXTRACT (kg/ha)	SOIL Al, KCl EXTRACT (ppm)	TOTAL SOIL Ca (kg/ha)	SOIL Ca, NH_4OAc EXTRACT (kg/ha)	SOIL Ca, NH_4OAc EXTRACT (ppm)	FOLIAR Ca, CANOPY TREE (ppm)	TOTAL SOIL P (kg/ha)	SOIL P, AVAIL. P. (NH_4F EXTRACT) (kg/ha)	SOIL P, AVAIL. P. (NH_4F EXTRACT) (ppm)	FOLIAR P: CANOPY TREE CONC. (ppm)	FOLIAR P: UNDERSTORY TREE FERN CONC. (ppm)
I. Pāhoehoe—poorly drained (wetland dieback)	1	Org	4.5	89.4	710	299.8	108.5	878	n.d.	197	5.0	43	n.d.	n.d.
	3	Org	4.1	93.2	820	193.5	5.3	59	7,700	157	2.0	18	613	878
	11	Org	4.8	64.7	338	590.0	109.3	560	9,400	182	3.7	18	443	896
	27	Org	5.1	25.1	115	1,058.0	103.1	333	9,100	251	6.1	10	523	860
II. Pāhoehoe—well drained (dryland dieback)	13	Org	4.5	3.6	42	558.3	33.4	325	8,200	99	0.9	9	376	566
	14	Org	4.3	26.1	180	714.4	22.4	160	8,600	120	1.2	8	409	928
III. ʻAʻā—poorly drained (wetland dieback)	43	Org	5.1	19.5	101	861.0	71.4	360	7,300	290	2.1	11	723	1,051
V. Eutrophic ash—coarse-textured (dryland dieback)	18	Org	5.5	11.3	41	1,301.4	20.6	83	9,900	178	1.5	6	438	1,073
		Min	5.9	13.6	23	2,203.7	106.8	156		230	1.2	2		
	20	Org	5.6	6.9	30	1,690.5	31.0	118	9,200	216	0.8	3	481	1,500
		Min	6.0	21.9	26	2,078.3	35.1	42		405	0.9	1		
	30	Org	5.6	1.4	3	2,567.4	68.9	159	9,600	437	2.1	5	580	n.d.
		Min	5.9	0.1	0	2,413.2	104.7	151		323	2.8	4		
VI. Eutrophic ash—fine-textured (displacement dieback)	22	Org	5.2	12.9	33	2,380.4	81.9	205	8,900	586	9.7	25	873	1,262
		Min	5.7	8.7	21	1,290.0	43.8	111		177	2.4	6		
	44	Org	5.2	14.6	34	2,049.5	139.2	322	8,900	706	6.4	15	707	980
		Min	5.7	0.6	1	1,332.7	94.6	206		227	1.7	4		
VII. Oligotrophic ash—(gap-formation dieback)	4	Org	3.5	71.4	510	168.1	5.3	39	7,000	170	1.0	7	616	958
		Org	3.7	n.d.	n.d.	81.0	9.7	71		124	0.2	1		
IX. Clay bogs—(bog-formation dieback)	17	Org	4.8	145.7	1,180	162.0	18.9	158	9,400	319	7.7	69	486	n.d.
		Org	4.8	251.1	1,365	167.0	26.3	141		426	11.2	59		
X. Organic soil bogs—(bog-formation dieback)	2	Org	5.1	72.2	694	280.0	40.7	313	n.d.	226	3.2	26	n.d.	n.d.
		Org	5.1	104.3	757	34.0	22.8	165		241	3.2	23		

NOTE: Habitat types IV and VIII are not included. Horizon depth is similar to that indicated in Table 2. The values are means of 5 independent composite samples for soils and means of 5–10 independent composite samples from mature leaves on healthy trees for foliar concentrations; n.d. = not determined; ppm = % multiplied by 10,000; ppm = μg/g.

TABLE 6

VARIATIONS IN SOIL AND FOLIAR CONCENTRATIONS OF MANGANESE AND IRON WITHIN AND BETWEEN VARIOUS HABITAT TYPES

HABITAT TYPES (DIEBACK TYPES)	RELEVÉ	HORIZON	HORIZON DEPTH (cm)	SOIL Mn		FOLIAR Mn		SOIL Fe		FOLIAR Fe	
				WATER EXTRACT CONC. (ppm)	NH_4OAc EXTRACT CONC. (ppm)	CANOPY TREE CONC. (ppm)	UNDERSTORY TREE FERN CONC. (ppm)	WATER EXTRACT CONC. (ppm)	NH_4OAc EXTRACT CONC. (ppm)	CANOPY TREE CONC. (ppm)	UNDERSTORY TREE FERN CONC. (ppm)
I. Pāhoehoe—	1	Org	0–10	2	7	n.d.	n.d.	19	43	n.d.	n.d.
poorly drained	3	Org	0–8	4	27	228	78	56	60	114	102
(wetland dieback)		Org	8–16	4	50			30	41		
	11	Org	0–8	1	5	195	156	146	8	110	113
	27	Org	0–9	1	13	133	73	27	30	114	90
II. Pāhoehoe—	13	Org	0–5	1	18	359	499	6	6	110	91
well drained	14	Org	0–6	1	1	528	224	2	10	112	93
(dryland dieback)											
III. ʻAʻā—poorly drained	43	Org	0–7	1	10	107	73	32	24	103	96
(dryland dieback)											
V. Eutrophic ash—	18	Org	0–7	1	1	146	72	4	1	114	84
coarse-textured		Min	7–12	1	21			5	4		
(wetland dieback)	20	Org	0–6	1	0	60	75	10	1	106	89
		Min	6–12	1	0			10	1		
	30	Org	0–10	1	1	21	75	12	13	106	n.d.
		Min	10–15	1	2			6	4		
VI. Eutrophic ash—	22	Org	0–10	1	4	50	74	32	13	106	93
fine-textured		Min	10–13	1	2			28	8		
(displacement dieback)	44	Org	0–12	1	5	81	75	34	20	112	91
		Min	12–16	1	2			22	11		
VII. Oligotrophic ash—	4	Org	0–7	1	5	204	98	116	34	104	103
(gap-formation dieback)		Org	7–12	1	20			116	10		
IX. Clay bogs—	17	Org	0–10	2	40	216	n.d.	14	24	126	n.d.
(bog-formation dieback)		Org	10–20	1	44			20	14		
X. Organic soil bogs—	2	Org	0–10	4	45	n.d.	n.d.	13	153	n.d.	n.d.
(bog-formation dieback)		Org	10–20	6	27			13	227		

NOTE: Habitat types IV and VIII are not included; n.d. = not determined; ppm = % multiplied by 10,000; ppm = μg/g.

well-drained pāhoehoe sites are younger than the poorly drained sites. The latter are also at the wetter end of the rainfall gradient. There is a further variation in that the well-drained pāhoehoe sites are situated at a higher elevation and thus experience a cooler temperature regime than the other shallow-soil sites.

Table 3 summarizes the organic carbon results together with three soil nitrogen parameters and two foliar nitrogen parameters. Organic carbon concentration values separate the habitat types into two broad groups. The eutrophic ash types show relatively low concentrations, varying from 11 to 13%, while all the other habitat types exhibit higher values, ranging from 15 to 41%. This trend correlates well with the pH values. It is interesting to note that the concentration of carbon in the bog soils does not exceed that recorded on the moderately drained oligotrophic ash soil. Organic carbon concentrations in the bog soils also are in the same range as on most shallow rock outcrop soils, indicating acid conditions and slow rates of decomposition. Organic concentrations in the surface mineral soil vary from only 1 to 3%. They are thus sharply separated from the organic overlays.

Organic carbon pool sizes reflect the combination of concentration, layer depth, and bulk density (BD), calculated as % carbon × BD × depth × 10,000. Therefore, shallow organic layers with high carbon contents can have the same pool sizes as deeper layers with lower concentrations. Within eutrophic ash sites, the coarser-textured soils have lower pool sizes (around 30,000 kg/ha) and the finer-textured soils have greater carbon pool sizes (around 50,000 kg/ha). As expected, the bogs have the greatest pool sizes, with 86,000–93,000 kg/ha down to 20 cm depth.

The concentration of total N correlates well with that of organic C ($r = .82$; $p < .01$). This means that 20% organic C contains about 1% total N, and 40% C about 2% total N. However, the higher-elevation relevés (13 and 14) contain somewhat less total N per unit of C (about 1.7% total N in 40% organic C), while the treeless bog relevé (2) contains somewhat more total N per unit C (2.3% total N in 40% organic C).

The C : N ratios give an indication of the potential rate of mineralization in the different sites. High ratios indicate potentially slow rates of mineralization. The slowest rates (C : N 27–30) were found in the higher-elevation shallow-soil sites (relevés 13 and 14). The fastest rates (C : N 11–13) were recorded for the eutrophic fine-textured soils (relevés 22 and 44). All other sites showed moderate rates (C : N 15–23), including the bog sites.

The concentrations of inorganic nitrogen (NH_4–N and NO_3–N + NO_2–N) are very dynamic and variable. The organic bog habitat exhibited outstandingly high percentages of NH_4–N, reflecting anaerobic conditions. The low values in the clay bog reflect the influence of telluric water. Nitrate–nitrogen quantities (here given as combined $NO_3 + NO_2$) were generally low (0–2 kg/ha) except in the eutrophic fine-textured sites, where they amounted to 6–7 kg/ha. Foliar N-levels are stated in the last two columns on Table 3 for the canopy tree species (*Metrosideros polymorpha*) and the undergrowth tree fern species (*Cibotium glaucum*). The tree ferns contain almost twice as much nitrogen in their foliage as the canopy trees in all habitats. *Metrosideros* exhibits a wide range of values from 6400 to 12,800 ppm. These values correlate significantly with total soil nitrogen and nitrate–nitrogen. The highest correlation was found with the nitrate–nitrogen concentration in the soil ($r = 94$; $p < .01$).

An interesting habitat variation is displayed in the canopy nitrogen–soil relationship. In the deep-soil habitat group, the lowest canopy nitrogen values were found in the eutrophic coarse-textured sites (type V, from 6500 to 7500 ppm) and the highest in the eutrophic fine-textured sites (type IV, from 11,400 to 12,800 ppm), while the oligotrophic deep-soil habitats (types VII and IX) showed intermediate values (from 7800 to 9300 ppm). This correlates with the substrate age sequence from recent to old as recorded on Table 2. A similar relationship is shown for the shallow-soil habitat group. The most recent pāhoehoe sites (13 and 14) have the lowest canopy nitrogen values (from 6400 to 7000 ppm), the intermediate-aged

sites (11, 27, and 43) have increasingly higher values, and the oldest site (relevé 3) again shows a value (9600 ppm) below that of the maximum (10,600 ppm) of a younger shallow-soil site (relevé 43).

Table 4 displays net mineralization and nitrate production rates for incubated soils. Net mineralization here includes the production of both ammonium– and nitrate (+nitrite)–nitrogen. One would expect net mineralization rates to be greater than nitrate production for the same sample. But this is not necessarily so, because of denitrification and other immobilization processes during incubation. Therefore, the two values are related, but are not always correlated. Each is considered a good estimate of nitrogen available to plants in the field.

The highest nitrogen mineralization rate (9.73 kg/ha) was found in the oligotrophic ash site (type VII), moderate rates occurred in the eutrophic fine-ash sites (4.15–4.70 kg/ha), while the eutrophic coarse-textured sites gave negative values. Negative mineralization rates also were recorded for most of the shallow-soil sites, except for the relevé on ʻaʻā lava.

The nitrogen production rates followed similar site-related trends, except that the highest values were recorded for the organic soil bog (relevé 2). However, in this case, the laboratory values may be overestimating actual nitrogen availability in the field. The same may apply to the relatively high value obtained for the poorly drained pāhoehoe site of relevé 1.

In general, nitrogen availability was low on the pāhoehoe (types I and II) and recent ash sites (type V). Consistently higher values were generated for the fine-textured (older) deep-soil habitats (types VI and VII) and for the ʻaʻā lava habitat (type III).

Table 5 lists the values for soil analyses for three chemical elements: Al, Ca, and P. These are presented together because of their strong interaction with soil pH. In addition, foliar analysis data are given for Ca and P.

Potassium chloride extractable soil Al varies in our samples from <100 ppm to >1000 ppm. Particularly low amounts of Al (<50 ppm) were found in all eutrophic ash soils (coarse and fine textured), which also were only weakly acid (pH 5.2–6.0). The oligotrophic ash habitat (type VII), with its extremely acid (pH 3.5) organic soil layer, showed more than ten times as much Al (510 ppm). However, this is still a moderate amount. Large amounts of soluble Al were recorded in the clay bog (>1000 ppm), but high values (>600 ppm) were also recorded in the organic soil bog (type X) and in the geologically oldest and poorly drained pāhoehoe sites (relevés 1 and 3). In contrast, the geologically more recent, poorly drained pāhoehoe sites (11 and 27), which also were somewhat less acid, had moderate to low amounts of Al. In spite of still greater acidity (pH 4.3 and 4.5), the well-drained pāhoehoe sites (type II) also had moderate to low amounts. Obviously, in addition to pH, drainage and substrate age interact in determining the amount of soluble Al.

Calcium was analyzed for its total and extractable amounts in the soil as well as for its concentration in the canopy foliage of *Metrosideros*. In terms of total Ca there is a clear habitat relationship in three groups. The eutrophic ash habitats showed the highest amounts, ranging from 1200 to 2600 kg/ha. The shallow-soil habitats (types I, II, and III) formed the second group, with Ca amounts from <200 to >1000 kg/ha. The oligotrophic ash habitats (including the bogs) had the lowest levels, from <50 to <300 kg/ha, and in their upper range overlap with the lower range of the second group.

Extractable Ca behaved almost inversely to the total amounts stored in the organic surface layers. In the eutrophic ash habitats (types V and VI), which had the highest amounts of total Ca, the extractable fraction varied from 1.5 to 6.8%. Similar low amounts were recorded for the well-drained pāhoehoe sites (13 and 14); however, these contained less total Ca. In contrast, greater fractions (from 8.2 to 36%) characterized the poorly drained pāhoehoe and bog sites. The lower organic layer in the organic bog (relevé 2) displayed the maximum proportion of 67% extractable Ca. However, here the total Ca was extremely low, with only 34 kg/ha. Two of the sites did not conform to this inverse relationship. They combined low extract-

ability with low levels of stored Ca. These were relevé 3 (poorly drained pāhoehoe) and relevé 4 (oligotrophic ash), which both had extremely acid pH values (under 4.2). Therefore, extractable Ca seems to be at higher levels in poorly drained sites than in better-drained sites, except where total stored Ca is already very much depleted in combination with extreme acidity.

Foliar Ca in the *Metrosideros* canopy was also low, with values from 7000 to 7700 ppm in the very acid sites (relevés 4 and 3, respectively). In the less acid eutrophic habitats (types V and VI), foliar Ca ranged from 8900 to 9900 ppm; and on the more acid well-drained pāhoehoe (type II), Ca ranged from 8200 to 8600 ppm. In general, the variation in foliar Ca between habitat types was not so great as one would expect from the greater variations displayed in the soil.

Soil P was analyzed in a similar manner, that is, as total stored in the soil layer and amounts extractable and presumably available to plants. Within the deep-soil habitat series, total P values displayed three levels. The highest values (586–706 kg/ha) were associated with the eutrophic fine-textured sites (relevés 22 and 44), intermediate levels (178–437 kg/ha) with the eutrophic coarse-textured sites (relevés 18, 20, and 30), and a low value (170 kg/ha) with the oligotrophic ash site (relevé 4). In the shallow-soil habitats, still lower values (99–120 kg/ha) were associated with the well-drained pāhoehoe sites (relevés 13 and 14), while the poorly drained rock outcrop sites displayed moderate values (157–290 kg/ha), overlapping in part with the eutrophic coarse-textured ash sites. The bog sites also contained moderate or intermediate amounts of total P (226–426 kg/ha). The fraction of P extractable or available to plants is relatively low (as compared to Ca) and varied from 0.5 to 2.5% of the total.

Available P follows a pattern similar to that of total P. Three ranges can be recognized again in the deep-soil habitats. Highest availability (6.4–9.7 kg/ha) was found in the eutrophic fine-textured sites, lowest availability (0.2–1.0 kg/ha) in the oligotrophic ash site, and intermediate availability (0.8–2.1 kg/ha) in the eutrophic coarse-textured sites. In the shallow-soil habitats, moderately high availability (2–6.1 kg/ha) was found in the poorly drained rock outcrop sites, while the well-drained pāhoehoe sites displayed low values (0.9–1.2 kg/ha). The bog sites had rather high values (3.2–11.2 kg/ha).

Foliar P showed consistently higher concentrations in tree fern fronds than in the *Metrosideros* canopy foliage. In several cases, more than twice as much P was concentrated in the tree ferns. As expected, the highest foliar P levels in *Metrosideros* were found in the eutrophic fine-textured ash sites (707–873 ppm). Surprisingly, the oligotrophic ash habitat (type VII) was associated with a higher foliar P level (616 ppm) than the eutrophic coarse-textured sites (type V, with 438–580 ppm). The lowest levels (376–409 ppm) were found in *Metrosideros* growing on well-drained pāhoehoe (type II).

Table 6 presents the soil and foliar concentrations of Mn and Fe. Soil Mn was analyzed by two methods: water extraction and ammonium acetate extraction. The first is a measure of Mn currently in the soil solution; the second measures potentially available Mn.

In the water extracts, Mn levels were the same (1 ppm) in most habitats, except in the geologically older and poorly drained pāhoehoe sites (relevés 1 and 3) and in the bogs. In these sites, Mn levels increased to a maximum of 4 and 6 ppm, respectively. Ammonium acetate extracts yielded higher levels of Mn than the water extracts, particularly in the bog sites where they rose to a range of 27–45 ppm and in the older, poorly drained pāhoehoe sites where they increased to a range of 7–50 ppm. In the geologically more recent, poorly drained sites (relevés 11, 27, and 43), the ammonium acetate extracts yielded moderate levels (5–13 ppm). Surprisingly, one of the well-drained and more recent pāhoehoe sites (relevé 13) yielded a moderately high level (18 ppm) and one of the young eutrophic ash sites (relevé 18) yielded 21 ppm in the surface mineral soil. In the other eutrophic ash sites, the mineral surface layers contained only up to 2 ppm. As expected, the older oligotrophic ash site (relevé 4) showed a moderately high amount (20 ppm) in its organic layer. In

general, soil Mn was high in the bogs and poorly drained rock outcrop soils, while low levels prevailed in the better-drained sites. But among the latter, unexpectedly high levels were found in two sites (relevés 13 and 18), both of which exhibited radical tree dieback of the dryland variety.

It is interesting that the foliar concentration of Mn in surviving *Metrosideros* trees was also high in these two dieback sites, with 359 ppm in relevé 13 and 146 ppm in relevé 18. However, another very high value (528 ppm) was recorded for the second stand on well-drained pāhoehoe in relevé 14, which so far has not yet developed canopy dieback. In general, again, foliar Mn concentrations showed moderately high levels (107–228 ppm) in all poorly drained sites and in the oligotrophic ash site (relevé 4), while moderately low levels (21–81 ppm) were recorded for the eutrophic ash sites, with the exception of relevé 18.

Soil Fe also was analyzed by the two methods of water extraction and ammonium acetate extraction. However, the second, presumably more radical, extraction method in most cases yielded the same or a lesser amount of soluble Fe except in the organic bog soil. The two methods complement each other in revealing the level of Fe available to plants.

In the shallow-soil series (types I, II, and III), the water-extracted Fe values form three clusters: low values (2–6 ppm) for the well-drained pāhoehoe sites, moderate values (19–56 ppm) for the poorly drained sites, and one outstandingly high value (146 ppm) for one of the poorly drained pāhoehoe sites (relevé 11). Similarly in the deep-soil series (types V, VI, and VII), the water-extracted Fe values form three clusters: low values (4–12 ppm) for the eutrophic coarse-textured ash sites (which are also well-drained), moderate values (22–34 ppm) for the eutrophic fine-textured ash sites, and a very high value (116 ppm) for the oligotrophic ash site (relevé 4). Surprisingly, the bog sites yielded only low to moderate Fe quantities (13–20 ppm) in the water extracts.

The ammonium acetate extracts of Fe gave similar trends with three exceptions. These were outstandingly high quantities (153–227 ppm) for the organic bog, only moderate values (10–34 ppm) for the oligotrophic ash, and a low value (8 ppm) for the poorly drained pāhoehoe site (relevé 11), which, however, gave the highest value by water extraction. In these three cases, we believe that the higher values, regardless of extraction method, are probably more indicative of the soluble Fe that may affect root growth in these soils.

The foliar Fe concentrations were generally somewhat greater in the *Metrosideros* canopy than in the tree fern fronds, but in both plant types they were remarkably constant within and between habitat types. There was only a slight correlation to the soil Fe pattern—i.e., somewhat more foliar Fe concentration on the poorly drained than on the better-drained sites. The highest foliar value (126 ppm) was recorded for *Metrosideros* from a bog site.

DISCUSSION

Now we ask, in what way do these data contribute to or argue against the original notion of eutrophic versus oligotrophic nutrient regimes in the habitat classification? And what do these soil and foliar chemical analyses explain about canopy dieback?

Habitat Classification and Nutrient Relationships

The separation at the first level into deep-soil and shallow-soil habitats at a mean depth of 50 cm, although arbitrary, emphasizes a fundamental physical difference. However, it does not separate the habitat types by the soil chemical parameters analyzed in this study, except for the eutrophic fine-textured deep-ash type (VI), which is unique.

In the deep-soil series, five parameters supported the simple two-way classification into eutrophic and oligotrophic habitat types. These were pH, organic C, total soil N, total Ca, and to some extent also extractable Ca. Other parameters indicated that a three-way breakdown would seem more appropriate.

The eutrophic coarse-textured type (V) is clearly not as high in available nutrients as originally thought. This was indicated by the C : N ratio (moderately high, 13–19), low NO_3–N, zero N mineralization and NO_3 production (upon soil incubation), and low to moderate levels of available P.

This lower nutrient availability, however, does not render the coarse-textured deep-soil habitat (type V) oligotrophic on our relative scale. The oligotrophic ash habitat (type VII) was distinct in several ways: by its extreme acidity (pH <4) and by its high levels of the potentially toxic elements Al, Mn, and Fe, which are not shared with type V. The oligotrophic ash habitat ranked much higher in N availability. Its N mineralization rates surpassed even those in the eutrophic fine-textured habitat (type VI). However, P availability was much lower in the oligotrophic type (0.2–1 kg/ha) than in the eutrophic type (6.4–9.7 kg/ha).

On account of these differences it appears justified to maintain the classification oligotrophic for type VII, but to change the designation of the coarse-textured ash habitat from eutrophic to mesotrophic. It may be noted also that this new three-way nutrient regime breakdown of the well to moderately drained deep-ash soil habitats coincides with their substrate ages; that is, mesotrophic for the youngest (191 yr), eutrophic for the intermediate-aged (1000 yr), and oligotrophic for the oldest (>4000 yr).

This still leaves the bog habitats, which also were designated as oligotrophic deep-soil habitats. It is interesting that they were not as acid (pH 4.8–5.1) as the moderately drained oligotrophic ash type. They also gave high N mineralization rates; and their extractable Ca levels were relatively high (18.9–40.7 kg/ha), although their total Ca levels were low. More surprisingly still, their quantities of available P ranked among the highest (3.2–11.2 kg/ha), but they were also highest in extractable Al (particularly the clay bog), they showed high levels of Mn (higher than type VII), and they showed high levels of ferrous Fe, particularly the organic bog (153–227 ppm). On a world scale these bogs are probably not oligotrophic. Moreover, they are not the most extreme Hawaiian bogs. They are situated on the east slope of Mauna Kea and have some lateral surface drainage and may receive nutrients in telluric water. However, we hesitate to redesignate their nutrient regime classification at this time until further work on other Hawaiian bogs may require reclassification.

The shallow-soil habitats had not been classified into nutrient regime types prior to this study. The present study allows a nutrient regime characterization and classification. Among the three shallow-soil habitat types here sampled, the poorly drained ʻaʻā (type III) displayed the most favorable nutrient relations. Its soil acidity was moderate (pH 5.1); and its NO_3–N content (2 kg/ha), N mineralization, NO_3 production rate (3.12 kg/ha), and total P content (290 kg/ha) were the highest among the shallow-soil types. Its extractable Ca level was nearly as high as in the eutrophic fine-textured deep-soil sites. The amounts of potentially toxic soluble forms of Al, Mn, and Fe were relatively low.

A certain discontinuity was found within the poorly drained pāhoehoe type (I), which separated into those relevés on the older lava (>3500 yr) and those on the younger lava (about 1500 yr). The latter (relevés 11 and 27) ranked close to the ʻaʻā habitat type (III) in their less extreme soil pH (4.8–5.1) and in their moderate levels of soluble Al, Mn, and Fe as compared to the older sites. However, this age-related variation within the pāhoehoe habitat type was not as pronounced as the nutrient differences (pH, organic C, total N, total and extractable Ca) between the pāhoehoe and ʻaʻā types. The ʻaʻā type was definitely richer in nutrients. The two poorly drained pāhoehoe sites on the older lava (relevés 1 and 3) differed primarily from the sites on younger pāhoehoe by yielding greater amounts of soluble Al, Mn, and Fe and by more acid soil reactions (pH 4.0–4.5).

The well-drained and youngest pāhoehoe sites (type II, about 500 yr) shared with the older poorly drained sites (type I) very acid soil reactions, but in contrast, had low levels of potentially toxic Al, Mn, and Fe. In addition, the young, well-drained sites had particularly low levels of available P (0.9–1.2

kg/ha). All pāhoehoe sites were low in NO_3–N (in contrast to the 'a'ā site), and their incubated N mineralization and NO_3 production rates were negative or very low.

It seems, therefore, that all pāhoehoe sites analyzed in this study can be classified as oligotrophic. The slightly more favorable nutrient relations in the younger poorly drained pāhoehoe sites (relevés 11 and 27) do not seem to warrant grouping these with the 'a'ā site. The latter (type III) should be classified as mesotrophic—i.e., between eutrophic and oligotrophic—on the relative scale used here. However, the 'a'ā habitat is mesotrophic for different reasons than the newly classified mesotrophic deep-soil habitat type (V). For example, the latter has very little, in fact almost no, NO_3 production potential, which renders it a more stressful habitat type than the poorly drained 'a'ā site.

Canopy Dieback and Soil–Foliar Nutrient Relationships

Canopy or stand-level dieback has been reported on all the habitat types analyzed (Mueller-Dombois et al. 1980). Therefore, no simple nutrient stress relationship can explain the phenomenon across the habitat spectrum. We have singled out N and P stresses as contributing factors in the dryland and gap-formation dieback types, and soil toxicity as a possible stress in the wetland and bog-formation dieback types.

Of particular importance here is to re-examine the soil–foliar nutrient relationships. Foliar N was particularly low (6400–7500 ppm) in the two well-drained and geologically most recent sites (types II and V). This low foliar N level correlated with the extremely low N supplying capacity in the soils of these habitats. They are the sites on which we noted dryland dieback. In these two habitat types, foliar P was also very low (376–580 ppm), and this correlated with a low soil P supplying capacity. The N and P levels reported are generally lower than the values given for similar forests elsewhere (e.g., Grubb 1977, Tanner 1977). These relationships, coupled with moisture stress, argue strongly for the N and P limitation theory in dryland dieback, which Kliejunas and Ko (1974) discovered experimentally on a very young site in a pioneer stand. However, their stand was atypical in comparison to the more mature and taller-stature dieback stands, which characterize the dieback territory in general and which were sampled in our study. Vitousek et al. (1983) reported similar conclusions with respect to nitrogen stress in tall-stature *Metrosideros* stands.

It should be noted here that our sample stands show different dieback conditions. On habitat type II, relevé 13 had undergone radical stand dieback, while relevé 14 was still unaffected. On habitat type V, relevé 18 had undergone radical stand dieback, relevé 20 was in partial breakdown condition, and relevé 30 was still unaffected. We noted earlier that in relevés 13 and 18, soil Mn levels were particularly high (18 and 21 ppm, respectively). High Mn levels were also reflected in the *Metrosideros* foliage of surviving trees on the dieback plots. It is possible that in these plots Mn toxicity added to the N and P stresses, predisposing these stands further to dieback. However, relevé 14, which did not yet undergo canopy dieback, also had very high foliar Mn, but its soil Mn was low. According to Andrew (1978), alternate soil wetting and drying can produce excess Mn just as constantly poor drainage does. It is possible, therefore, that Mn levels fluctuate in the well-drained rain forest sites and, when temporarily excessive, may act as potential dieback "triggers."

Gap-formation dieback was described for stands on moderately drained oligotrophic ash, such as relevé 4 (habitat type VII). Between 1976 and 1980, we witnessed canopy dieback in relevé 4 (which on the vegetation map is still classified a closed forest). Here, N limitation cannot be considered. Instead, low P and other nutrients associated with acid soil, such as low Ca and high levels of soluble Al, Mn, and Fe, can be considered to impose stresses on the stand.

Total soil P (170 kg/ha) and available P (1 kg/ha) in the oligotrophic ash site were lowest among the three deep-soil habitats. The eutrophic fine-textured type showed the highest level (total soil P, 600–700 kg/ha;

available P, 6–10 kg/ha). The available soil P trend correlates with the soil age sequence, i.e., moderately low in the younger (191 yr) ash soils, peaking in the mid-aged (1000 yr), and declining in the older (>4000 yr) soils. This trend of available P first increasing and later decreasing with soil aging supports the conclusions of Walker, Thompson, and Jehne (this issue) and Walker et al. (1981), who reported such trends for Australian dune soils.

Soil Ca behaves in a similar way, except that it starts at a high level in the young soils and then declines drastically with advanced age. In this connection it is of interest to note that Ca in the mineral soil exceeded the amount in the organic overlay in the youngest soils (habitat type V), while in the mid-aged and older soils (types VI and VIII) higher Ca amounts were found in the organic overlay. This indicates a nutrient shift from subsoil to surface by recycling, which comes about in the early stages of soil development.

The amounts of soluble Al, Mn, and Fe were all high enough in the oligotrophic ash habitat to be considered toxic under agricultural conditions. For example, Clements (1980) and Clements and Putman (1972), working on toxicity levels in Hawaiian soils, found 15–20 ppm soil Al to be toxic to wheat seedlings grown in salt solution. While allowances for detoxifying interactions must be made for natural soils, the high value of 510 ppm of soluble Al in the oligotrophic ash site indicates at least toxicity potentials. Similarly, the level of soluble Mn of 20 ppm in the oligotrophic ash soil exceeded the toxicity threshold of 7 ppm given by Hoyt and Nyborg (1971) for *Medicago sativa*. Further, Clements (1980) reported that sugar cane growth is severely reduced when the Mn level in the sheath tissue exceeds 100 ppm. *Metrosideros* leaf tissue on the oligotrophic ash contained 204 ppm.

Ferrous Fe toxicity has been reported for crop plants (Clements and Putman 1972, Martin 1968) at a level of 30 ppm. This was far exceeded with the 116 ppm in the oligotrophic ash soil. Therefore, if nutrient stresses play a role in the gap-formation dieback recognized for habitats on oligotrophic ash, they are quite different from those identified for dryland dieback, where N and P stresses were considered most important. In gap-formation dieback, P and Ca limitations and to a still greater extent Al, Mn, and ferrous Fe excesses appear to contribute to the nutrient stress complex.

In wetland dieback, which occurs mostly on poorly drained pāhoehoe, available N is again probably a limiting factor. This was indicated by the high C : N ratios and the generally low N mineralization and NO_3 production rates. Increased denitrification due to poor aeration may impose additional losses of NO_3 (Balasubramanium and Kanehiro 1976), and N limitation may be further aggravated by the inability of *Metrosideros* roots to function at full capacity under waterlogged conditions. These unfavorable conditions are reflected in the low levels of foliar N in some sites (relevé 11) where the substrate was waterlogged. Nitrogen limitation may also enforce nutrient conservation through internal translocation. This would result in the maintenance of relatively high foliar N levels despite low levels of available N in the soil as seen in other sites (relevé 3). Internal recycling of mobile nutrients (particularly N) is thought to be an adaptive mechanism (Golley 1983) on oligotrophic soils, where the mature vegetation has become decoupled from its soil nutrient supply. The vegetation then is maintained by tight recyling of nutrients and by atmospheric input.

Soluble Al, Mn, and Fe are also at toxic levels in the wetland dieback areas. This toxicity may be considered a manifestation of waterlogging and low pH values. It therefore supports indirectly the earlier view of Mueller-Dombois et al. (1980) that poor drainage following a root flooding event may be a cause of wetland dieback.

In bog-formation dieback, N and P are probably not limiting in the substrate, but the trees' roots cannot function adequately under continuously poor aeration and the consistently high levels of soluble Al, Mn, and Fe, which in turn may limit the trees' capacity for absorption of the available N, P, and Ca. Here, even the nutrient conserva-

tion mechanisms may not function anymore. This is indicated in the clay bog (relevé 17), where the foliar N level is low despite a moderate level of mineral N production in the surface soil.

As an endemic tree species, *Metrosideros polymorpha* has probably evolved a certain tolerance to otherwise toxic levels of soluble Al, Mn, and Fe. For example, dominant, mature *Metrosideros* trees decrease in height from oligotrophic ash (17–19 m tall) with about 500 ppm soluble Al, to poorly drained pāhoehoe (15–17 m tall) with up to 800 ppm soluble Al, to bog habitats with over 1000 ppm Al, where trees are stunted and grow only 1–2 m tall. Physiological tolerance mechanisms to metal toxicities suggested in the literature (e.g., Thurman 1981) include biochemical detoxification at the root level. Maintenance of such tolerance mechanisms requires energy beyond that needed for organic production. As a result, height growth may become stunted as displayed in the bog habitats. A creeping, mat-forming fern (*Dicranopteris linearis*) that grows abundantly in the more open wetland and bog areas (Mueller-Dombois et al. 1980) may be considered here as a temporary habitat detoxifier because of its high capacity for Al accumulation (Moomaw, Nakamura, and Sherman 1959).

Soil toxicity may also restrict *Metrosideros* seed germination and seedling establishment on the poorly drained sites. For example, Tanner (1977) found that the inhibition of seed germination on very acid tropical montane rain forest soils from Jamaica was probably related to soil toxicities caused by low pH. This may explain in part the finding (Mueller-Dombois et al. 1980) that on poorly drained pāhoehoe and in bog habitats, *Metrosideros* reproduction occurs either by seedlings growing on logs or by vegetative means.

Displacement dieback has been described for stands growing on the eutrophic fine-textured ash habitat (Mueller-Dombois et al. 1980). Here, reestablishment of the canopy *Metrosideros* is inhibited by high seedling mortality prior to the sapling stage, primarily because of the dense shade formed by the vigorous tree fern undergrowth (Burton and Mueller-Dombois 1984). Our results show that relatively favorable levels of pH, N, P, and Ca prevail in this habitat type, and that potentially toxic elements occur only at rather low and probably insignificant levels. Ideally, therefore, the canopy trees should not experience any nutrient stress. However, a certain nutrient stress may be imposed by the tree ferns via root competition for available N and P. This deduction is made from the much higher foliar levels of these nutrients tied up in the tree ferns versus the canopy trees.

CONCLUSIONS

Our analysis has clearly demonstrated that despite the chemically uniform basaltic volcanic soil-parent materials on which the Hawaiian *Metrosideros* rain forest has developed, the underlying organic soil layers are by no means uniform. The broad spectrum of physically different habitats recognized earlier is matched by an equally broad spectrum of soil chemical variations. However, for the purpose of maintaining a simple reference frame, we have enlarged the earlier two-way classification of oligotrophic and eutrophic soil nutrient regimes only by one additional category. Young ash sites were recognized as mesotrophic on account of their moderate pH and high Ca levels and because of their low levels of N and potentially toxic quantities of soluble Al, Mn, and Fe. Old ash sites were recognized as oligotrophic because of their extreme acidity and high levels of potentially toxic metals. Intermediate-aged ash sites were determined as eutrophic because of their favorably balanced soil nutrients.

Among the lava rock outcrop habitats, the ʻaʻā type was recognized as mesotrophic on account of its relatively balanced soil nutrients. However, the pool sizes of available N, P, and Ca were below those of the eutrophic ash habitat, and the potentially toxic elements were at higher levels. All pāhoehoe habitats were classified as oligotrophic; the well-drained type because of

its extreme acidity, its high C : N ratio, and extremely low supply of nitrogen; the poorly drained type because of its similarly low N supply and its additional limitation from consistently high levels of potentially toxic metals. Nutritionally, the bog habitat types were not as depauperate as originally thought, but were considered oligotrophic because of their constantly anaerobic conditions combined with very high levels of potentially toxic elements.

The canopy dieback phenomenon in *Metrosideros* stands, which occurs across this habitat spectrum in different manifestations, cannot be totally explained from this nutrient study. Since canopy dieback is recognized as a relatively sudden collapse, the dieback "trigger" must also be a suddenly operating or fluctuating site factor. Among the soil nutrients, the only factor of this sort may be the possibly fluctuating level of potentially toxic soil Mn discovered in the well-drained sites. However, it is possible also that gradually intensifying nutrient imbalances may lead to a tolerance threshold beyond which the canopy collapses. Yet, it appears more likely that the nutrient imbalances, as documented in this study for all but the eutrophic ash and 'a'ā lava sites, are more or less constant over several generations of *Metrosideros* canopy tree populations. Therefore, it is suggested that the imbalanced nutrient states become increasingly stressful with stand development, i.e., they may contribute to the loss of stand vigor that is expected with advancing age. Hence, nutrient stress may add to the preconditioning for canopy dieback. Moreover, since trees are forced to grow slowly on such nutritionally poor and imbalanced sites, their senescing life stage may be prolonged and thereby further synchronized.

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